THE TAXONOMIC POSITION OF *ACTINOPTERIS INDICA* SRIVASTAVA.

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(Plate x, A; three Text-figures.)

[Read 25th October, 1961.]

Synopsis.

A number of specimens of *Actinopteris indica* Srivastava from the Permian of Queensland were examined. Sufficient information was available to include the species in the family Calamitaceae.

This was based on the absence of a resistant cuticle, the presence of a pith cast in the stem supporting the leaves and the nature of the leaves.

There are a number of undoubted specimens of *Actinopteris indica* Srivastava in an undescribed flora from Baralaba Colliery, Central Queensland. They form part of the collection made firstly by Miss B. Houston, now of the Queensland Geological Survey, and later supplemented by specimens collected by the manager of the colliery. The collection has now been incorporated into the museum of the Geology Department, University of Queensland.

The specimens were collected from the roof of the Dawson Seam in the Upper Bowen Series of Permian age.

Baralaba lies approximately 70 miles south-west of Rockhampton.

CALAMITACEAE.

Actinopteris indica Srivastava. (Plate x, A; Text-figs 1, 2, 3*a*, 3*b*).

Actinopteris indica Srivastava, *Palaeobotanist*, 3, 1954, p. 72, fig. 4, pp. 74-76, Pl. 3, fig. 26.

Approximately 30 specimens of this species were present, some of which formed almost complete whorls. A few whorls were connected by what appeared to be a thin stem, but was probably a pith cast. These specimens were attributed to Srivastava's species without hesitation. They differed from the type specimen in only one respect, in that they were smaller. Size is not generally a critical factor in distinguishing species.

Certain additional information obtained from the specimens was considered sufficient to place the genus in the family Calamitaceae.

Srivastava described it as *incertae sedis*. He referred to Feistmantel (1876, p. 76) who described the genus using *A. bengalensis* Feistmantel as the type species. Feistmantel considered it to be a fern. Zeiller (1902) reclassified it as possibly a new genus of the Equisetales; he considered each leaf whorl to have been formed into conical verticils similar to those of *Schizoneura wardi* Zeiller, as illustrated on his plate 6, figs 5-9.

Differences in the whorls of each species are that the leaves of *S. wardi* were joined only near their bases, whereas the leaves of *A. bengalensis* were joined for more than half their length. As a verticil of *A. indica* was similar to *A. bengalensis* in this and most other respects, we may compare *A. indica* directly with *S. wardi*. The verticil of *Actinopteris* must have been almost flat (see text-fig. 1), for if it were not, at least some of the leaves would have split along their junction or have torn apart during compression. It is suspected from the apparent epidermal cell structure as seen under low-power magnification that the individual leaves of a whorl were completely fused along their junction. The apical angle formed by a verticil of *S. wardi* lay between 90° and 120°, measured from Zeiller's illustration (*loc. cit.*).

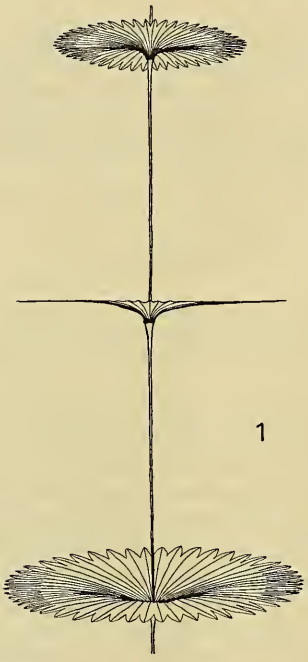
Arber (1905) and Dolianiti (1953) both shared Zeiller's opinion that *A. bengalensis* was probably not a fern, but a member of the Equisetales. Srivastava (1954) reviewed all evidence to date. After unsuccessfully endeavouring to prepare cuticles from a

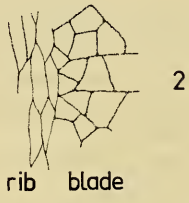
well-carbonized crust in a specimen of *A. bengalensis*, he concluded: "Is it possible that these plants do not possess a resistant cuticle? If this is so, then it is possible that Feistmantel was not altogether wrong in placing this plant in the ferns."

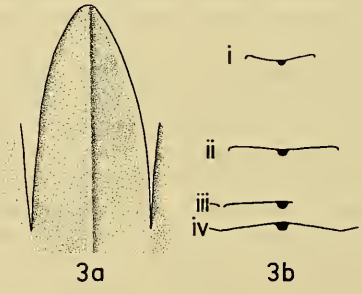
Schenk (1868), who described the genus *Actinopteris*, compared the nervation of the type species, *A. peltata*, with some recent ferns including *Trichomanes* species and *Lindsaya schomburgkii* Klotzsch. He excluded *A. peltata* from the genus *Cyclopteris*, where it had been placed previously, because of its orbicular nature.

The individual leaf whorls of *A. indica* contained from 46 to 52 leaves, each having a single, unbranched midrib, with secondary venation lacking.

The length of individual leaves measured from different whorls varied from 1·2 to 2·6 cm., but in most whorls the leaves were 1·7 cm. long (i.e., whorl 3·4 cm. in diameter). This is smaller than in the type specimen where they were 3 cm. long. The leaves were united for three-quarters of their length.







Text-fig. 1.—Reconstruction of part of a "branch" bearing verticils of *Actinopteris indica* Srivastava. The "branch" shown is the pith cast. The projection is natural size and in correct projection if the centre verticil were at eye level, and held six inches from the eye. The dimensions used are those of example 2, Specimen F31980 (see Plate x, A), as tabulated on Table 1.

Text-fig. 2.—Outlines of a few cells showing difference of structure in region of midrib, and of blade, in *Actinopteris indica* Srivastava. × 80 (approx.).

Text-fig. 3*a*.—The free portion of a single leaf of *Actinopteris indica* Srivastava viewed from below. × 7.

Text-fig. 3*b*.—Cross sections through the leaf of text-fig. 3*a* to show shape of leaf. × 7.

The most elliptical of the whorls is on specimen F31980 (this is the registered number of the specimen in the museum of the Geology Department, University of Queensland. All specimens described in this paper are housed in the museum of the Department). The individual leaflets vary in length between 1·7 cm. and 2·3 cm. Measured across the width of the leaf, at the point where the leaves become free, the leaf that was 1·7 cm. long was 3·0 mm. wide, and the leaf that was 2·3 cm. long was 2·1 mm. wide. Each leaf still had closely similar surface areas, so the ellipticity was probably caused during fossilization or subsequent folding of the beds.

Srivastava used, as one of his criteria to distinguish this species from *A. bengalensis* Feistmantel, a linear dimension (see his Table 1, p. 75, 1954). This criterion is not considered to be valid in distinguishing species, as size will depend on age of the plant and other factors, although if expressed as a ratio $\frac{\text{width of free segment}}{\text{length of leaf}}$ it may be valuable in undistorted specimens. His other criteria are sufficiently adequate to distinguish these species without any possible confusion.

The leaflets had slightly rounded acute apices (see text-fig. 3*a*), more acute than those illustrated by Srivastava. This appeared to be the only difference between the Indian and Australian specimens. The midrib appeared to reach the apex.

Each individual leaf was flexed slightly about the midrib downwards in the same direction as the side on which the midrib projected throughout the united part of the verticil. This is shown on text-fig. 3*b* (iv). The side with the midrib was assumed to be dorsal by analogy with published illustrations of other calamitalean foliage, i.e., the leaves were dorsiflexed. In the free part of the leaf, the edges were strongly enrolled, and the flexing of the leaf was away from the midrib. This is shown in the cross-sections of the leaf of text-figure 3*a*, varying from the united section of the leaf (text-fig. 3*b*; iv) towards the apex (text-fig. 3*b*; iii, ii and i). This made each whorl appear crenulate as well as being dentate. The crenulations may have been caused by slight distortion during compression, but as they were quite distinct on nine verticils, this would be unlikely. No leaf apices were found to have been folded during compression, so that the free portions of the leaves must have been sufficiently rigid to remain in the same plane as the united portion of the whorl, although the whole whorl was sufficiently thin not to tear when folded into the same plane as the supporting branch. The crenulations would add to this rigidity. No whorl was found where one-half of the verticil was folded back onto the other half. This, along with the slight distortion shown towards the centre of some verticils (e.g., the complete whorl in the lower centre of Plate x, A), supported the contention that they were slightly conical, as a cone would tear when folded.

The pith casts were ornamented with longitudinal striations; in specimen F31974 these appeared to be in paired groups. These represented vascular bundles. The internodes tapered gradually into the slightly swollen nodes. Two of the nodes appeared to have a series of small swellings around the leaf base. It was difficult to determine the relationship of these small swellings with the leaf parts, but they appeared to bear a relationship with the striations of the stem; they lay at either side of the paired vascular bundles. These were thought to represent swellings of the vascular bundles, where the bundles branched so as to give rise to the approximately 50 leaf midribs in each whorl. On specimen F31972 there was a suggestion of eight bunches of midribs in one verticil and seven in a second. If this were correct it would favour eight pairs of vascular bundles in the stem. Purely for mechanical reasons, the stem must have been considerably thicker than the pith cast. The thickening of the pith cast at the nodes appeared unusual.

No stems could be found, although their presence along the pith casts was evident. On Plate x, A, example 1 (the two incomplete verticils on the right hand side) shows a ridge in the upper, very incomplete verticil, which became a groove in the upper part of the lower verticil, then a ridge in the lower part of the same verticil. From the disposition of the midribs in each whorl it appeared that the tissue of the stem had vanished rapidly after deposition of the specimen, then the leaf had been pressed into the cavity formerly occupied by the tissue of the stem.

Another hypothesis that could be advanced to explain the identity of these specimens is that the pith casts represent a simple vascular cylinder or protostele covered by parenchymatous or other tissue and a cuticle that was not resistant to maceration. If this were so, then the vascular strands would not be visible. No tracheids were recovered, nor were any cell outlines visible in the pith casts.

The dimensions of a number of specimens are given in Table 1.

From this it appears that the plant bore slightly crenulate, flatly conical circular verticils of approximately 50 leaflets, united for three-quarters of their length, uninerved, with the nerve probably reaching the slightly rounded, acute apex. Stems having a very thin pith bore the verticils approximately at right angles separated by a distance of slightly less than one verticil diameter.

It would appear physiologically undesirable for such verticils to be borne any closer than this in a healthy plant because of shading. In other calamitalean genera the verticils appear to be borne at a distance approximately equal to one leaflet apart, *vide* numerous illustrations in Hirmer (1927). For the sake of stability, the stems were probably at least four times the thickness of the pith cast in the internode.

Only small fragments of calamitalean pith cast were found in the collection. They were too small for identification. Numerous other stems were found, but they were considered to be fern stems, probably belonging to *Sphenopteris* sp. *Sphenopteris* occurred frequently in the area.

TABLE 1.

Dimensions of several Specimens of Actinopteris indica *Srivastava.*

——	1	2	3	4
Length of internode	33	upper 34 lower 35	28	unknown
Diameter at centre of internode	0·6	upper 0·4 lower 0·4	0·4	0·7
Mean diameter verticil				
Upper	40	26	32	30
Middle	—	36	—	—
Lower	unknown	40	37	—
Diameter of node				
Upper	1·0	unknown	0·9	0·9
Middle	—	0·8	—	—
Lower	unknown	1·0	unknown	—
Number of striations across width of internode	not visible	not visible	not visible	8 in paired bundles

Note: All measurements are in millimetres. 1 and 2 are on specimen F31980 (see Pl. x, A), 3 is on specimen F31972, 4 is on specimen F31974.

The specimens were preserved in a grey shale as compressions with some of the carbonaceous material still present. Specimens could be removed as Canada Balsam transfers following the technique of Walton (1928), but all attempts at oxidation maceration, viz. Schulze maceration, or in bleaching solution resulted in complete oxidation of the plant material. This, in itself, would suggest that the plant was not a spermatophyte.

Maceration was also attempted in either HCl or saturated $ZnCl_2$, the latter following the suggestion of Harris (1932, p. 4) that modern fern cuticles were preserved during maceration in a non-oxidizing, non-alkaline solution.

The surface of these specimens was examined in reflected light. Some cell outlines could be seen with difficulty (see Text-fig. 2 and Table 2). The cells adjacent to the veins were elongated along the length of the veins, whereas the cells of the lamina were cubic or polygonal. Neither balsam transfers nor cellulose acetate peels showed any additional detail.

Some specimens from Newcastle, N.S.W., discovered by Etheridge (1895) and described by Arber (1905) as *Phyllotheca etheridgei* bear a certain resemblance to these specimens.

P. etheridgei consisted of a series of whorled verticils borne on a thick, ribbed stem. A comparison of this species with *A. indica* is given below using Etheridge's fig. 1, Plate xvii (fig. 1 was reproduced by Arber as text-fig. 9 on page 27) and fig. 3 of Plate xviii with the specimen of *A. indica* illustrated as text-fig. 1 in this paper.

Actinopteris indica Srivastava.	*Phyllotheca etheridgei* Arber.
50 leaves per whorl.	20 or more leaves per whorl.
Leaf apex rounded.	Leaf apex pointed.
Sheath absent.	Leaf bases united to form a sheath.
Leaves fused for three-quarters of their length.	Leaves fused for seven-eighths of their length.
V notch where leaves become free.	U notch where leaves become free.
Diameter of node less than one-tenth of the length of a leaf.	Diameter of node approximately one-quarter of the length of a leaf.
Internode shows no more than eight vascular bundles in side view.	Internode shows at least eight vascular bundles in side view.

These two species have the following characters in common: Leaf whorls approximately the same size; leaf whorl flatly conical; whorls spaced approximately one verticil diameter apart along the stem; each leaflet bears a single median nerve.

A. indica may be compared with *Annularia* spp., e.g., *A. stellata*. This plant has been figured by numerous authors, including Seward (1898, p. 339). A comparison of *Actinopteris indica* with *Annularia stellata* is given below. It may be seen that

TABLE 2.

Dimensions of Cells on Leaf Surface of Actinopteris indica *Srivastava.*

	On Blade.	Along Vein.
Leaf 1	range $\begin{cases} 37 \times 25 \\ 18 \times 12 \end{cases}$	90 × 8
Leaf 2	40 × 32	80 × 10
Leaf 3 (largest in collection)	32 × 22	63 × 8
Leaf 4 (smallest in collection)	55 × 40	90 × 16

All dimensions are in μ.

A. indica possesses more features in common with *A. stellata* than with *Phyllotheca etheridgei.*

The following features are distinctive between these two species:

Actinopteris indica Srivastava.	*Annularia stellata* Schl.
50 leaves per whorl.	Fewer than 25 leaves per whorl.
Leaf apex rounded.	Leaf apex often mucronate.
Leaves fused for three-quarters of their length.	Leaves free, bases united.
Whorls spaced approximately one verticil diameter apart along the stem.	Whorls spaced approximately one-half verticil diameter apart along the stem.
Leaf whorls tend to be ovate-orbicular	Leaf whorls tend to be orbicular with the attachment eccentric.

These two species have the following characters in common: Diameter of the node less than one-tenth of the length of a leaf; leaf whorls borne on a slender stem; leaf whorls approximately the same size; each leaflet bears a single median nerve; margin of free portion of leaflets is enrolled; leaf whorls (?) slightly ensheathing. It is because of these common features that *A. indica* has been included in the family Calamitaceae. This raises the point that *A. indica* should no longer be included in the genus *Actinopteris*, but should be transferred to some other genus such as *Annularia*, or to a new genus. *Annularia ivini* Walkom has its leaves united for most of their length as does *Actinopteris indica*. Etheridge (1895), in his description of *Phyllotheca etheridgei* Arber, has mentioned that "The intercostal spaces are also crossed by the finest possible transverse striae, arranged in a festoon-like manner". This feature is

closely similar to the striae in *Annularia ivini* (Walkom, 1941, Pl. viii), but is absent in *A. stellata* and *Actinopteris indica.*

From this it appears that *Actinopteris indica* possesses many characters similar to members of the genus *Annularia,* but that it also possesses certain quite distinctive characters.

Acknowledgements.

The writer wishes to thank Professor Dorothy Hill, Research Professor of Geology in the University of Queensland, for allowing him the opportunity to examine the Baralaba Collection, for placing at his disposal all facilities required to make this examination while on a short visit to the University and for making valuable suggestions to improve the manuscript. Thanks are also due to Dr. H. K. Worner, Director of Research, B.H.P. Central Research Laboratories, Shortland, N.S.W., for arranging to have the manuscript prepared for publication and to Mr. S. Thompson, of the same organization, for his excellent photography. The writer's indebtedness to Dr. A. B. Walkom for suggesting that the writer might be allowed to examine this material and for assistance in the references is also acknowledged.

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EXPLANATION OF PLATE X, A.

Specimen F31980. *Actinopteris indica* Srivastava, showing verticils described in the text. The two verticils of example 1 (Table 1) are those running in a line at about 60° to the horizontal, along the right-hand side. The large verticil in the top right-hand corner was not measured. The three verticils of example 2 are bisected by the fracture in the rock, with the smallest verticil at the top of the plate. The specimen was illuminated from the bottom right-hand corner. Natural size.